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Effects of experimental food supplementation on movements of juvenile northern goshawks (*Accipiter gentilis atricapillus*)

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Abstract Food availability is thought to strongly influence the leaving phase of natal dispersal in animals with condition-dependent dispersal. We conducted a food supplementation experiment to determine the influence of extra food on the onset of dispersal and early dispersal movement patterns of 42 radio-tagged northern goshawks (*Accipiter gentilis atricapillus*) from 28 broods in north-central New Mexico during 1992 and 1993. We randomly assigned half of the broods each year as treatments and the other half as controls. Treatment broods were given supplemental food from hatching (late April) until mid-October. Control broods received the same visitation rate but no food. Birds were located approximately every 2 days from fledging until mid-October in 1992 and 1993. Timing of fledging and independence were not affected by the treatment. However, extra food significantly influenced post-fledging movements of juvenile goshawks. During the late fledgling-dependency period (>65 days of age until independence) control birds were located in the natal area (<2 km from nest tree) more frequently than supplemented birds. This pattern reversed after independence (approximately 82 days of age) when supplemented birds were located more frequently in the natal area than controls. After independence the control birds were never located in the natal area and by the end of September in both years the controls had all left the study area (study area boundaries were approximately 25 km from nest tree). Supplemented birds were never located outside of the study area for the duration of the experiment. We conclude that the control birds dispersed out of the study area and the supplemented birds

remained. Since the experimentally fed juveniles remained near a known food source and the controls did not, our study demonstrates that food availability influences at least the first 4 months of post-fledging movement patterns in this population. These results also suggest individuals base dispersal decisions on knowledge of their environment at a local scale, which can influence juvenile recruitment.

Keywords *Accipiter gentilis* · Breeding chronology · Condition-dependent dispersal · Excursions · Food supplementation

Introduction

Natal dispersal is the process by which individuals move from their natal area to where they reproduce or would have reproduced had they survived and mated (Howard 1960; Greenwood 1980; Johnson and Gaines 1990; Stenseth and Lidicker 1992). Because natal dispersal involves a complex series of movements (Walls and Kenward 1995, 1998), the final natal dispersal distance is a function of the cumulative history of movements during the dispersal process (Dufty and Belthoff 2001; Wiens 2001). We agree with Dufty and Belthoff (2001) that natal dispersal refers to events that occur within a distinct ontogenetic stage of development and that, once completed, do not occur again. In altricial birds, natal dispersal would describe the series of events that begin at fledging and end when the bird obtains its first nest area.

Movements of juveniles away from their natal areas can influence the spatial and genetic structure of populations and the evolution of social behaviour (Greenwood 1980; Arcese 1989; Wiens 1996). Dispersal of both juveniles and reproductive adults also links subpopulations in spatially heterogeneous environments and hence is a critical factor in dynamics of metapopulations (Pulliam and Danielson 1991; Bollinger et al. 1993; Wiens 1996).

Author order is alphabetical to reflect the collaborative nature of this research project

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Despite its importance, natal dispersal is poorly understood. Many factors appear to affect dispersal. One environmental factor thought to strongly influence the onset of natal dispersal in animals with condition-dependent dispersal is food availability (Ims and Hjermann 2001). Variation in timing and distance of natal dispersal in these organisms may be related to differential ability of the young to acquire food in natal areas (Dufty and Belthoff 2001). Animals may move if food resources have been locally depleted or if there is potential for more food resources elsewhere (Bennetts and Kitchens 2000). Alternatively, some animals exhibit exploratory movements (often referred to as excursions) during times of high food availability (Nilsson and Smith 1985; Gonzalez et al. 1989; Ferrer 1993; Walls and Kenward 1995, 1998). Excursions may be a mechanism to identify the location of food or other resources during periods when they are not food stressed. In addition, the information gained during excursions may be important in the eventual success in foraging and gaining a breeding site (Waser 1985; Bennetts and Kitchens 2000; Green and Cockburn 2001).

Our ability to clearly identify causal relationships between environmental factors such as food availability and the onset of natal dispersal is limited because few field experiments have been conducted that simultaneously manipulated food supplies and monitored the fate of dispersing individuals with radio-telemetry. Manipulating food supplies allows us to deconfound naturally correlated variables that could affect natal dispersal such as weather and local food availability. Tracking radio-tagged birds allows movements to be studied in greater detail and over wider areas than can be accomplished by resighting banded birds (a common approach in avian dispersal studies; Koenig et al. 1996).

The few experiments that have been conducted have had inconsistent results. Food supplementation has delayed the onset of dispersal movements in some organisms (Frumkin 1994; Kenward et al. 1993; Bustamante 1994; Kim 2000), advanced dispersal in others (Willey and van Riper 2000) and had no effect on timing of dispersal in other organisms (Veltmann 1989; Bustamante 1994). Previous supplemental feeding experiments that have had a treatment effect on dispersal timing have only delayed dispersal, not prevented it. The influence of natal area food supplies on distances juveniles move from the natal area is also unclear. Longer post-fledging movements have been reported for better nourished animals (Ferrer 1992, 1993), yet in some studies juveniles from areas with abundant prey moved shorter distances than those from areas of low food availability (Newton 1986; Sonnerud et al. 1988).

In this study, we evaluate the influence of food availability on the initiation of natal dispersal and subsequent post-fledging movement patterns of juvenile northern goshawks (*Accipiter gentilis atricapillus*, hereafter referred to as goshawk). By monitoring the movements of radio-tagged juveniles from supplemented and control nests, we test the hypothesis that juvenile

goshawks disperse from natal areas with poor environmental conditions and remain on or close to natal areas when resource conditions are suitable.

Materials and methods

The study species

The goshawk is a large (735–1364 g) forest raptor, occupying boreal and temperate forests throughout the Holarctic (Squires and Reynolds 1997). It often nests and hunts in old-growth or mature forests, which creates potential conflicts in the management of public forest lands for timber production versus goshawk conservation. Although the goshawk currently has no federal protection in Canada, Mexico or the United States, there have been several petitions to list the goshawk as threatened or endangered under the U.S. Endangered Species Act. Its status has been (and still is) the object of considerable litigation in the United States (Kennedy 1997). Management plans developed to reduce the risk of timber harvest to goshawk populations are focused on managing breeding season prey populations (e.g., Reynolds et al. 1992). This approach is based on the assumption that goshawk populations are regulated by breeding season food availability. This study is part of a series of investigations exploring the influence of breeding season food availability on goshawk demographics (Ward and Kennedy 1996; Dewey and Kennedy 2001).

The goshawk's annual cycle is typical of many temperate raptors. The breeding season begins from mid-February through early April and lasts until the young are independent in late August–early September. Our study was conducted from hatching (April) through the first 2 months of the non-breeding season.

Goshawks are: socially monogamous; territorial, noncolonial, synchronous breeders; and their nests are >1 km apart. They rarely breed as yearlings and most breeding birds are ≥2 years old (Squires and Reynolds 1997). Typical of taxa with similar life histories, they are long-lived (maximum age in the wild is 19 years; Kenward et al. 1999) with high breeding site and mate fidelity (Woodbridge and Detrich 1994).

The degree of philopatry in goshawks, as in most birds, is unknown because resighting rates of banded juveniles is low (1–2%) and other methods, such as satellite telemetry or genetic analyses, have not been used to estimate dispersal rates. However, the fact that female and male goshawks have been documented nesting within 25 km of their natal area in several populations (Squires and Reynolds 1997) including this study population (P.L. Kennedy and J.M. Ward, unpublished data) indicates some level of philopatry. The species is also a partial migrant; some individuals and populations are resident year-round, whereas others migrate seasonally. Local winter food availability and climate likely influence whether or not a bird migrates or resides in the breeding area year-round (Squires and Reynolds 1997; C.W. Boal, D.E. Andersen and P.L. Kennedy, unpublished data). The relationship between natal dispersal and migration movements is unknown in a partial migrant like the goshawk because it is difficult to determine if juveniles are searching for food or breeding areas or both. Since dispersal trajectories are more than just the simple linear pathway between natal area and first breeding area (Wiens 2001), we assume all juvenile movements occurring prior to first breeding are part of the natal dispersal process. We also assume these early life movements influence distances from natal to first breeding site.

Food supplementation experiment

From April through October in 1992 and 1993, we conducted a food supplementation experiment using 28 goshawk broods from a population in the Jemez Mountains in north-central New Mexico. The study area is 6,452 km² in size; its boundary was defined as the perimeter of the Jemez Mountains (see Siders and Kennedy 1996

for details on the study area). We conducted this experiment to determine if there was a causal relationship between prey availability and growth and survival of young goshawks (Ward and Kennedy 1996); here we analyse effects of supplementation on their movements.

Our experimental methods are briefly described below. Experimental details are reported in Ward and Kennedy (1994, 1996) and Ward et al. (1997). Trade name products are mentioned to provide complete descriptions of methods. The authors' institutions neither endorse these products nor intend to discriminate against products not mentioned.

In 1992, six of 12 active nests were randomly assigned as treatments and six as controls. Sixteen active nests were located in 1993, with eight randomly assigned as treatments and eight as controls. Eight of these 16 nests were occupied by one or both adults in both years (see Table 1 in Ward and Kennedy 1996 for details on territory occupancy). We observed behaviour of the incubating adult bird to determine date of hatching. Food supplementation began the day after hatching in 1992 and a few days prior to hatching in 1993 (mid-April), and ended in mid-October in 1992 and 1993. Japanese quail (*Coturnix coturnix*) were provided every other day on solar-powered, feeding podiums located 10 m from the nest. All feeding podiums were equipped with a motorized cover triggered by a solar sensor to hide the food at dark and expose it again at daylight (podium design is detailed in Ward et al. 1997). This allowed us to leave enough food for several days without attracting predators that might take the food or prey upon the goshawks. Non-motorized podiums also were placed at control nests and visited at the same interval and for the same amount of time to standardize the level of disturbance.

To maximize treatment effect, we provided as many quail as supplemented broods would take in addition to the amount required to meet 100% of the juveniles' estimated daily energetic requirements (Ward and Kennedy 1994, 1996). Adults and juveniles were observed taking quail at every supplemented nest from fledging until experiment termination.

Timing of fledging and independence

In the original experimental design (Ward and Kennedy 1996) *fledging* was defined a priori as the first observation of young perching on a branch (we assumed the same fledging age for all young in a nest). We also assumed that a juvenile goshawk was self-feeding if it was not located in the natal area for a week and was still alive (a juvenile raptor will starve within 7 days if not fed by its parents; Kirkwood 1981). So, *independence* was defined a priori as the first time a juvenile spent more than a week at least 2 km away from its nest. This is comparable to the definitions used by Marquiss and Newton (1981) and Kenward et al. (1993) for European sparrowhawks (*A. nisus*) and European goshawks (*A. g. gentilis*), respectively. Dates of independence were determined for each juvenile in a nest.

Kenward et al. (1993) reported that fledgling goshawks typically stay within 300 m of the nest for 65 days post-hatching, at which time their flight feathers harden and they are capable of extended flight. For the movement analyses, we used 65 days of age as a dividing point between the two phases of the pre-independence, post-fledging period: *early fledgling-dependency* (fledging until day 64) and *late fledgling-dependency* (day 65 until independence).

Monitoring post-fledging movements

Nine-gram transmitters with mortality switches (Advanced Telemetry Systems, Isanti, Minn., USA) were attached to the tarsi of 42 nestling goshawks at approximately 21 days of age [13 supplemented birds (at 5 nests) and 16 controls (at 6 nests) in 1992; 10 supplemented birds (at 4 nests) and 3 controls (at 2 nests) in 1993 (there were fewer controls in 1993 because of low nestling survival; Ward and Kennedy 1996)]. The 1992 sex ratios [$m/(m+f)$] of

nestlings at 21 days were 0.56 for controls and 0.61 for supplemented birds. In 1993 the sex ratios were 0.33 for controls and 0.57 for supplemented birds.

Birds were relocated thereafter at least every 2 days by one or two observers from the ground. By mid-August the birds started moving long distances from the nest; we continued to locate birds every other day on the ground and also tracked their movements from an airplane at least once a week until mid-October in both years. We estimated that each point location (acquired from ground or aerial telemetry) had a 500-m radius error associated with it (based on the observer's ability to locate transmitters placed throughout the study area). Each bird was monitored until: (1) the transmitter failed, (2) the transmitter detached from the tarsus, (3) the bird died, (4) the bird disappeared from the study area, or (5) the experiment was terminated.

Aerial searches for dispersing goshawks were conducted by flying a series of N-S transects spaced from 10–15 km at altitudes of approximately 200–500 m above ground level. We searched for birds until all birds were located or until we reached 30–40 km beyond the study area boundary in all directions. This region beyond the study area was characterized by low elevation pinyon-juniper (*Pinus edulis* – *Juniperus* sp.) habitat, which is not suitable for goshawk nesting (Siders and Kennedy 1996), but is suitable for foraging (Squires and Reynolds 1997).

Based on known spacing of multiple alternative nest sites within goshawk territories (Woodbridge and Detrich 1994; Dewey et al. 2002), all locations within 2 km of the nest were considered to be within the natal area and we refer to it as *natal area*. Locations ≤ 25 km from the nest are defined as *inside the study area* and locations >25 km from the nest are referred to as *outside the study area*. We used 25 km as a cut-off point because most nests were located within 25 km of the study area boundary, which occurred where the montane habitat of the Jemez Mountains transitioned into low elevation, pinyon-juniper habitat. We assume movements outside of the study area are movements away from the natal breeding area.

Data analyses

Timing of fledging and independence

To evaluate the influence of natal food supply on the onset of dispersal we compared the timing of fledging and independence between supplemented and control groups. Age at fledging and independence and Julian dates of these events were compared using the PHREG procedure in SAS (SAS Institute 1991) using treatment and year as explanatory variables. The PHREG procedure implements a multiple regression analysis based on Cox's (1972) semi-parametric, proportional hazards model. This type of failure time analysis is widely used to evaluate the effect of explanatory variables on the occurrence and timing of events (Muenchow 1986). Although brood size has been correlated with timing of fledging in other avian species (e.g., Kenward et al. 1993; Ellsworth and Belthoff 1999), our sample size prevented us from including brood size as an additional explanatory variable. To ensure statistical independence among observations of fledging and dispersal (Massot et al. 1994), we analysed the age and date of these two events using nest as the experimental unit. For age and date of independence, the brood average of these two variables was analysed. To evaluate model validity, we tested the assumption of constant proportionality using the Wald chi-squared statistic (Muenchow 1986; SAS Institute 1991). It was not statistically significant ($P>0.05$) in all analyses, indicating the assumption was not violated in any model.

Post-fledging movements

In these analyses we wanted to answer three questions:

1. Do juveniles make more excursions out of the natal area during the late fledgling-dependency period as compared to the early

- fledgling dependency period and were these movements influenced by supplementation?
2. Did supplementation influence the tendency of juveniles to leave the natal area prior to and after independence?
 3. Did supplementation influence the dispersal of birds from the study area?

We used a single mixed model ANOVA (PROC MIXED; Littell et al. 1996) to address questions 1 and 2. For question 1, we compared the proportion of locations within the natal area versus beyond the natal area (but within the study area) between the early and late fledgling-dependency periods. For question 2 we compared the proportion of locations within the natal area versus beyond the natal area (but within the study area) between the late fledgling-dependency period and post-independence. We were interested in assessing treatment, year, sex, and period as fixed-effects factors. A nest served as the experimental unit for treatment and year; a bird (nested within nest), as the experimental unit for sex; and a repeated measure through time on a bird, as the experimental unit for period. Random-effects terms in the model were specified accordingly. However, not all nests contained birds of both sexes, so it was not possible to fit a full four-way factorial mixed model. Preliminary analysis of the effects of sex, year, treatment, and year \times treatment interaction (using averages computed over all periods as data in the analysis) did not support significant effects of sex, year, year \times treatment interaction (sex: $F_{1,6}=0.04$, $P=0.855$; year: $F_{1,9}=0.19$, $P=0.674$; year \times treatment: $F_{1,9}=2.31$, $P=0.163$); thus, the factors sex and year were omitted from the final analysis. Fixed effects in the final model were treatment, period and their interaction; random effects were nest(treatment) and period \times nest(treatment). We transformed the response variable using an arcsine square root transformation to better meet the assumptions of normality and homogeneity of variance. Comparisons of least squares means using t -tests were used to assess pairwise differences among mean transformed proportions; contrasts of least squares means were used to assess components of the treatment \times period interaction.

We addressed question 3 by comparing the proportion of aerial telemetry bird locations within the study area after independence by treatment using logistic regression in PROC GENMOD. The GENMOD procedure fits a generalized linear model to the data by maximum likelihood estimation (SAS Institute 1999). Effects due to year, sex, and year \times treatment interaction were non-significant thus, data were pooled between sexes and years in subsequent analyses (year: $\chi^2=1.8$, $df=1$, $P=0.2$; sex: $\chi^2=1.1$, $df=1$, $P=0.3$; year \times treatment: $\chi^2=2.8$, $df=1$, $P=0.1$). Treatment and nest(treatment) were the effects analysed in the final model. The nest(treatment) variable in GENMOD also accounts for potential correlations in sibling movement patterns. PROC GENMOD was used instead of PROC MIXED in this analysis because we were not constrained by multiple repeated measures (only one period was involved in this analysis – post independence); PROC GENMOD is not effective at analysing complex repeated measures designs (P. Chapman, personal communication). Also, GENMOD is designed to analyse binomial data such as proportions so a transformation of the response variable is not necessary (White and Bennetts 1996). We used an α -level of 0.05 for all statistical tests and we report $\bar{x} \pm SE$ unless otherwise specified. All analyses were conducted in SAS Version 8 (SAS Institute 1999).

We summarize distances moved from the nest graphically (Figs. 1, 2). We did not analyse these distances statistically because we could not estimate distance if birds were outside the study area. This study area boundary effect could result in biased (failure to include movement distances of >55–65 km) distance distributions. Thus, we did not think an analysis of distance from nest would provide any meaningful information for a species that is quite capable of moving distances >65 km after the breeding season (Squires and Ruggerio 1995).

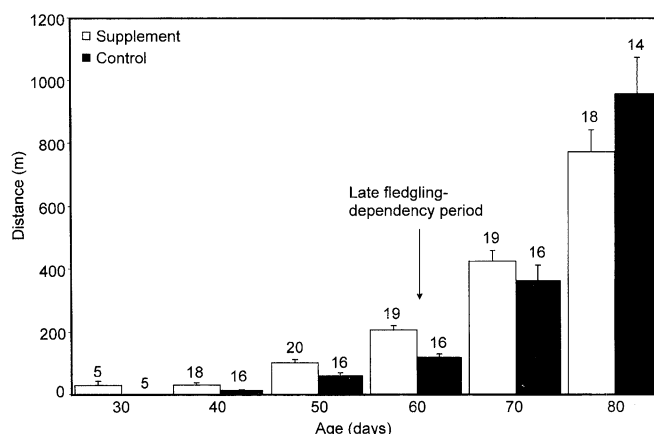


Fig. 1 Average distance (m) from nests of supplemented and control juvenile goshawks prior to independence (fledging to approximately 82 days of age) in the Jemez Mountains of New Mexico during 1992 and 1993. The number above each bar is the number of individual birds located and the bars are standard errors. The numbers on the x-axis are the midpoint ages for each 10-day interval

Results

By the late nestling period (prior to fledging) in 1992 and 1993 we were still tracking the fate of 29 (12 nests) and 12 birds (10 nests), respectively (see Ward and Kennedy 1996 for details on individual fates). In 1992 transmitters failed on four control birds and seven supplemented birds by early September. Three control birds died during the early-fledgling dependency period of 1992. We successfully tracked 15 and 12 birds for the majority of the experiment in 1992 and 1993, respectively (Table 1). At the time the experiment was terminated, we could still locate ten birds in 1992 (six supplemented; four controls) and eight birds in 1993 (eight supplemented; 0 controls).

Timing of fledging and independence

Although there was a tendency for supplemented young to fledge earlier than controls in both years, the effect was not significant ($\chi^2=0.9$, $df=1$, $P=0.3$). Timing of fledging also did not vary between years ($\chi^2=0.8$, $df=1$, $P=0.4$). Mean fledging age (pooled over both years) of supplemented and control birds was 39.5 days and 41.5 days, respectively.

Supplemented birds also did not reach independence at a significantly earlier age or earlier date than controls (age: $\chi^2=0.3$, $df=1$, $P=0.6$; date: $\chi^2=0.7$, $df=1$, $P=0.4$). Age and date of independence also did not vary between years (age: $\chi^2=1.3$, $df=1$, $P=0.3$; date: $\chi^2=3.2$, $df=1$, $P=0.1$). Mean age of independence for supplemented and control birds (pooled over both years) were 83 days and 80.8 days, respectively. All control birds and 81% of supplemented birds reached independence by 14 weeks of age. The remaining 19% of supplemented birds were independent by 15 weeks of age. Median date of

Table 1 Sampling effort and average proportion of supplemented (S) and control (C) locations (\pm SD) within the natal and study area of juvenile goshawks in the Jemez Mountains, New Mexico during 1992 and 1993

Year / treatment (n^a)	Early fledgling ^b			Late fledgling ^c			Post-independence ^d		
	Attempts ^e	Natal area ^f	Study area ^g	Attempts	Natal area	Study area	Attempts	Natal area	Study area
1992: S (7)	14.9 \pm 1.5	97.1 \pm 13.4	2.9 \pm 5.3	11.0 \pm 1.2	61.0 \pm 15.5	6.5 \pm 6.9	11.0 \pm 1.2	61.0 \pm 15.5	6.5 \pm 6.9
1992: C (8)	13.1 \pm 2.6	100.0 \pm 0.0	0.0 \pm 0.0	13.9 \pm 2.4	84.7 \pm 15.3	0.9 \pm 2.5	21.6 \pm 6.1	1.7 \pm 2.4	18.5 \pm 14.6
1993: S (9)	13.8 \pm 2.9	95.2 \pm 15.2	4.8 \pm 12.0	13.2 \pm 5.9	79.0 \pm 34.3	6.7 \pm 4.5	34.8 \pm 11.8	18.8 \pm 9.3	35.5 \pm 24.2
1993: C (3)	12.7 \pm 4.0	100.0 \pm 0.0	0.0 \pm 0.0	10.7 \pm 1.2	84.4 \pm 9.4	3.1 \pm 5.4	19.3 \pm 11.6	0.0 \pm 0.0	3.4 \pm 3.0

^a n = the number of juveniles tracked throughout the experiment

^b Early fledgling-dependency period = fledge day – day 65

^c Late fledgling-dependency period = day 66 – independence

^d Post independence=independence until last location or experiment termination

^e This column represents the average number of times we tried to locate an individual bird

^f This is a proportion which was calculated per bird as: number of locations/number of attempts. Natal area includes locations ≤ 2 km from the nest.

^g This is a proportion which was calculated per bird as: number of locations/number of attempts. Study area includes locations > 2 km from the nest, but ≤ 25 km from the nest. The sum of natal area and study area proportions will not add up to 100 % because birds were not always located during each attempt.

independence for controls was 22 August (range 4 August–2 September) and the median date for supplemented birds was 16 August (range 5 August–9 September).

movements between treatments after independence, and the lack of difference between treatments during the early fledgling-dependency period, contributed to the significant period and treatment*period interaction.

Post-fledging movement patterns

Do juveniles make more excursions out of the natal area during the late fledgling-dependency period as compared to the early fledgling dependency period and were these movements influenced by supplementation?

The majority of birds from both treatment groups were located within 200 m of the nest during the early fledgling dependency period (Fig. 1). As they grew older, birds from both treatment groups made more excursions away from the natal area. While there was no overall effect of supplementation on bird movements, we did observe a difference in the movement behaviour of the birds during the late fledgling-dependency period: supplemented birds made more forays away from the natal area than control birds during this time (treatment: $F_{1,11}=1.08$, $P=0.32$; period: $F_{2,22}=215.36$, $P<0.001$; treatment \times period: $F_{2,22}=17.11$, $P<0.001$; Table 1).

Did supplementation influence the tendency of juveniles to leave the natal area prior to and after independence?

Birds from both treatment groups were located significantly more frequently out of the natal area after independence compared to the late fledgling-dependency period (contrast of treatments between late-fledgling dependency and post-independence: $t_{22}=-5.16$, $P<0.001$; Figs. 1, 2). However, supplemented birds continued to be located in the natal area after independence while control birds were not (Fig. 2). The dramatic difference in

Did supplementation influence the dispersal of birds from the study area?

Supplemented juveniles were also located significantly more frequently within the study area than the controls during the post-independence period ($\chi^2=4.07$, $df=1$, $P=0.04$). By 17 weeks of age, 6 of the 7 control birds that could be located were >20 km from their nests (Fig. 2). The other control bird was 13 km from its nest. In 1992 a control bird was caught at a migration trapping

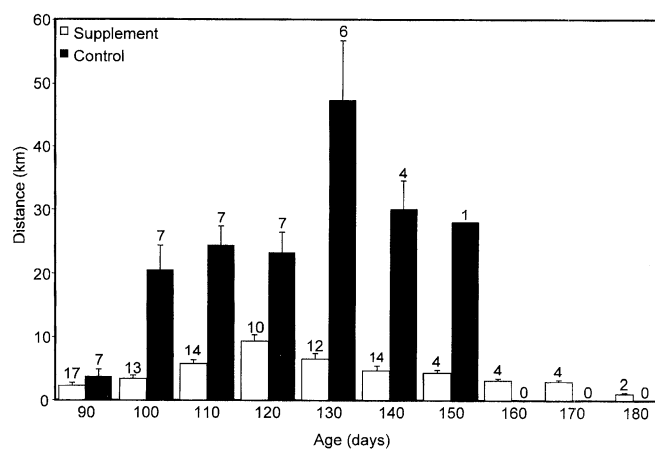


Fig. 2 Average distance (km) from nests of supplemented and control juvenile goshawks after independence (approximately 82 days of age) until data collection terminated (approximately 140 days of age in 1992 and 80 days of age in 1993) in the Jemez Mountains of New Mexico during 1992 and 1993. The number above each bar is the number of individual birds located and the bars are standard errors. The numbers on the x-axis are the midpoint ages for each 10-day interval

station about 130 km south of the study area 12 weeks after it had fledged (S. Hoffman, Hawkwatch International, personal communication). Supplemented birds were rarely located >10 km from their nests after independence (Fig. 2) and for the duration of the experiment, they were never located outside the study area. In contrast, most control birds left the study area or if they were located, it was in the low elevation pinyon-juniper habitat surrounding the Jemez Mountains. The effect of additional food was most dramatic in 1993 when 45% of supplemented bird locations (18.8% of total attempts; Table 1) were <3 km from their nest at age 14 weeks post-fledging. In contrast, both control birds had dispersed out of the study area by this time and their last known locations were 69 and 33 km from their nest at age 11 weeks post-fledging. In 1993 we continued to monitor the movements of all juveniles until the end of November; none of the supplemented birds had left the study area by this time and neither of the controls was relocated within the study area.

Discussion

The influence of extra food on onset of dispersal

Why did additional food not influence the onset of dispersal in this experiment? Our lack of treatment effect on timing of independence is similar to the findings of Veltman (1989) who found no effect of supplemental food on the timing of independence in Australian magpies (*Gymnorhina tibicen*). However, our results are contrary to other experimental studies that did find extra food advanced timing of independence (e.g., Nilsson and Smith 1985; Kenward et al 1993). Rate of transition from fledging to independence occurs as a function of the changes in two parallel processes, parental provisioning and self-feeding, but the interaction of these two processes during that transition is not well understood (Yoerg 1998). In supplemental food experiments such as ours, where food is placed near nests, the additional food may augment parental provisioning until the young begin to self-feed. Although we did not measure parental provisioning in this study, it is possible that parents reduced their provisioning at supplemented nests in response to reduced juvenile food demand, i.e., lowered begging rates (observed in food supplemental experiments by Cook and Hamer 1997; Weimerskirch et al. 1997; Wiehn and Korpimäki 1997; and Hamer et al. 1998). Thus, the lack of treatment effect on timing of independence in our experiment might be a result of undocumented changes in parental provisioning.

Alternatively, natal food supplies might not have a strong influence on timing of dispersal because supplemental food did not influence the juveniles' onset of self-feeding and their hunting success rates. Yoerg (1998) investigated factors correlated with age of independence of European dippers (*Cinclus cinclus*) and found most of the age variation was explained by the juvenile dippers'

foraging success during initial attempts at self-feeding and during the transition to independence. Unfortunately we do not have the observational data necessary to evaluate onset of self-feeding in our sample but this would be an excellent topic of future research.

Was there a potential experimental effect on the supplemented birds' ability to self-feed? Adult and juvenile goshawks will use dead quail provided at nests. Supplemented nestlings were heavier in this experiment (Ward and Kennedy 1996) and in a similar experiment conducted in Utah (Dewey and Kennedy 2001). Would early experience with abundant dead quail interfere with the juveniles' ability to self-feed? In 1993 we stopped the supplementation during the third week of October and continued to monitor the fate of birds until 30 November. All supplemented birds that could be located at the end of the experiment were alive at the end of November and had not left the study area. These observations suggest the young could self-feed and the experiment did not interfere with their ability to forage and thus, their survival.

The influence of extra food on post-fledging movements

Although extra food did not influence timing of fledging and independence, it had a significant effect on juvenile movement patterns both pre- and post-independence. Supplemented juveniles made more excursions prior to independence than did controls. The control birds' movements fit the traditional model of natal dispersal: remain in the natal area until independence and then permanently leave the natal area after independence. However, dispersal out of the study area did not occur with supplemented offspring because they were relocated near their nests consistently throughout the fall and were observed taking quail from the podium after independence. Clearly supplemented juveniles returned to their natal area because it was a reliable food source.

Juvenile control birds moved outside of the study area both years before the end of the experiment, and a control bird was caught along a migration route in 1992, confirming that control birds dispersed out of the study area and supplemented birds remained. As mentioned earlier, all supplemented birds actually remained on the study area until approximately 5 weeks after the experiment ended in 1993 suggesting the experiment influenced their dispersal strategy at a larger scale. Juveniles in this population appear to disperse from areas with poor environmental conditions and remain on or close to the natal territory when resource conditions are suitable. These results also support the inherent assumption that dispersers monitor their environment at a local scale to make dispersal decisions. These results do not support the hypothesis that well-nourished juveniles dispersed more than less nourished young (Ferrer 1993; Massot and Clobert 1995).

Our results are also different from those of Kenward et al. (1993) who noted that European goshawks neither made excursions in the post-fledging period nor continued

to use natal areas in winter. Unlike European goshawks, other raptors make excursions and appear to take time to assess areas beyond their natal area before settling in a new home range or returning to their natal area (Walls and Kenward 1995; Bennetts and Kitchens 2000). For taxa with dynamic and unpredictable food resources such as many predators, excursions might be advantageous when food supplies are high. This enables species like the goshawk to explore potential habitats when risk of starvation is minimal. However, when food supplies are not over abundant, i.e., the controls, the expected gains in familiarity with potential habitat is not worth the energy and/or risk associated with constantly moving (Bell 1991; Baker 1993; Bennetts and Kitchens 2000).

Although we did not monitor birds past November, our data indicate that a sufficient food supply could prevent dispersal at least during the juveniles' first autumn. The effect of 6-months food augmentation on the juveniles' final dispersal distances is unknown. None of the juveniles was relocated on the study area in subsequent years nor have they been reported as breeders in other monitored populations. Unfortunately, we discontinued investigations in the study area in 1995, just as some of these juveniles might have entered the breeding population.

Few studies have investigated the linkages between post-fledging movements and natal dispersal distance (J.R. Belthoff, personal communication; J.A. Wiens, personal communication). However, two studies that monitored movements of fledglings to their natal dispersal site demonstrated that early dispersers tended to settle significantly farther from their natal area than did late dispersers [common buzzard (*Buteo buteo*), Walls and Kenward 1995; brown thornbill (*Acanthiza pusilla*), Green and Cockburn 2001]. Juvenile brown thornbills that delayed dispersal were four times more likely to recruit into the local breeding population than juveniles that dispersed early. Similar data were not available for the buzzard. The factors influencing the dispersal patterns were not documented in the two studies, but our data demonstrate that juveniles from nest areas with abundant food are more likely to delay dispersal. We would predict that young from the food-abundant natal areas are more likely to disperse shorter distances and be recruited into the natal population.

To examine the effect of natal area food supply on the entire natal dispersal process further experiments are needed. Animals could be fed throughout the winter to determine if sufficient food supplies would prevent dispersal in the following spring, which has been documented in common buzzards (Walls and Kenward 1998). The fate of individual animals could be monitored beyond study area boundaries with satellite transmitters which are small enough to use on animals >600 g and can monitor global movements (Britten et al. 1999; Webster et al. 2002). A greater challenge to investigations of dispersal is to use the experimental results to predict the dispersal process of many organisms that are faced with

changes in their food resources by landscape-level anthropogenic activities.

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ERRATUM

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Effects of experimental food supplementation on movements of juvenile northern goshawks (*Accipiter gentilis atricapillus*)

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In the Materials and methods section, under Food supplementation experiment, 3rd paragraph, 3rd sentence: Table 1 in Ward and Kennedy 1996 should not have been linked in the online version.

In Fig. 2: the number over the second bar from the left should be 10 and not 7.

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